

## Performance of Two Strains of Lake Trout Stocked in the Midlake Refuge of Lake Michigan

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**Abstract.**—To evaluate the performance of Seneca and Marquette strains of lake trout *Salvelinus namaycush* for restoring stocks in southern Lake Michigan, we compared relative abundance (fish per lift of 305 m of gill net), survival (slope of the decline in natural logarithms of relative abundance), growth (von Bertalanffy growth curves), and wounding rates by sea lamprey *Petromyzon marinus* of the 1984 and 1985 year-classes captured at ages 3–16 in fall gill-net assessments on the Sheboygan Reef and the Milwaukee nearshore area during 1987–2000. Marquette strain lake trout survived at a significantly higher rate than Seneca strain lake trout prior to age 3 but at similar rates after age 3. The 1984 year-class of lake trout survived at a significantly higher rate than the 1985 year-class of lake trout prior to age 3 but at similar rates after age 3. Emigration of lake trout from the Sheboygan Reef to the nearshore Milwaukee area was similar for the Marquette and Seneca strains but was higher for the 1984 year-class than the 1985 year-class. The mean relative abundance of the 1984 and 1985 year-classes of Marquette and Seneca strains of lake trout varied erratically with age but did not decline with age on the Sheboygan Reef and Milwaukee nearshore area. On the Sheboygan Reef, growth in length, expressed as asymptotic length ( $L_{\infty}$ ), differed significantly between the Marquette and Seneca strains of lake trout but did not differ significantly between the 1984 and 1985 year-classes. On the Sheboygan Reef, wounding rates by sea lampreys did not differ significantly between the Marquette and Seneca strains of lake trout among size-classes (633–734, 735–836, and  $\geq 837$  mm) during 1994–2000. Our findings suggest that the performance of Marquette strain lake trout was superior to that of Seneca strain lake trout on the Sheboygan Reef in central Lake Michigan.

Lake Michigan once supported the most productive lake trout *Salvelinus namaycush* fishery in the world (Holey et al. 1995). Lake trout yield from Lake Michigan declined slowly from the late 1800s through the early 1900s, presumably because of excessive fishery exploitation (Hansen 1999). Then, during 1943–1949, yield declined rapidly from 954.5 metric tons to 104.5 metric tons, through the combined effects of fishery exploitation, predation by the sea lamprey *Petromyzon marinus*, and habitat degradation (Hansen 1999). By 1950, the world's most productive lake trout fishery was gone.

Rehabilitation of lake trout in Lake Michigan began in 1965 with the release of 1.1 million hatch-

ery-reared yearlings and lakewide chemical treatment of larval sea lamprey populations (Holey et al. 1995). Stocking increased steadily until the early 1970s and then leveled off at about 2.4 million yearlings/year (Holey et al. 1995). The first complete round of chemical treatment of larval sea lamprey populations effected an 80–90% reduction in adult sea lamprey abundance by 1966 (Holey et al. 1995). Adult lake trout abundance subsequently increased but failed to produce self-sustaining adult populations. Potential causes of failed natural reproduction include excessive mortality from fishing and sea lampreys, changes in the fish community, low adult lake trout density, and excessive contaminant burdens in adult lake trout (Holey et al. 1995).

The adoption of a lakewide management plan (LWMP) in 1985 created a more coordinated focus for lake trout rehabilitation efforts in Lake Mich-

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TABLE 1.—Stocking date, number stocked, average weight, and coded wire tag (CWT) retention rate for the 1984 and 1985 year-classes of Marquette (MQ) and Seneca (SEN) strain lake trout stocked on the Sheboygan Reef as yearlings in 1985 and 1986.

Year-class	Strain	Stocking date(s)	Number stocked	Average weight (g)	CWT retention rate (%)
1984	MQ	May 29, 1985	61,480	17.5	93.0
		Jul 10–14, 1985	333,922	21.6	93.0
	SEN	May 29, 1985	61,510	15.3	96.2
		Jul 10–14, 1985	318,497	19.7	96.2
1985	MQ	Jun 11 and 13, 1986	336,346	19.5	90.8
	SEN	Jun 11 and 13, 1986	238,780	17.1	95.7

igan (Holey et al. 1995). Strategies that were adopted by the various management agencies included a cap on total annual mortality, the use of four types of rehabilitation zones, specific stocking rates for each zone, the evaluation of multiple lake trout strains, and a coordinated assessment of progress toward objectives of the plan (Holey et al. 1995). One of the measures designed to reduce total annual mortality on lake trout was the creation of refuges in northern and southern Lake Michigan (Holey et al. 1995). The southern refuge, the focus of this study, encompasses 2,859 km<sup>2</sup> around the Midlake Reef Plateau; this area is composed of four, relatively deepwater reefs (40–80 m) popularly known as the Sheboygan, Northeast, East, and Milwaukee reefs (Holey et al. 1995). Historically, the Midlake Reef Plateau was among the most productive spawning areas for lake trout in Lake Michigan (Coberly and Horrall 1980; Brown et al. 1981; Holey et al. 1995; Dawson et al. 1997).

The stocking strategy incorporated in the LWMP in 1985 called for the use of “lean” strains that spawn in deep (30–85-m) water in habitats such as the Midlake Reef in Lake Michigan (Holey et al. 1995). Among the lean, deepwater spawning strains identified for use in Lake Michigan was the Seneca Lake strain, which spawns in the deep waters of Seneca Lake, New York (Krueger et al. 1983). The Marquette strain, derived from Lake Superior shallow-water lean lake trout and used extensively for stocking in Lake Michigan, was designated as a standard for comparison with other strains (Krueger et al. 1983). The LWMP called for paired releases of Marquette and Seneca strain lake trout in the Midlake Refuge for five consecutive years, beginning with the 1984 year-class (Holey et al. 1995). An outbreak of epizootic epitheliotropic disease virus (Bradley et al. 1988; Bradley et al. 1989; McAllister and Herman 1989) resulted in the destruction of broodstocks and hatchery dis-

infections in 1988. As a result, the only paired releases of Marquette and Seneca strain lake trout in the Midlake Refuge were the 1984 and 1985 year-classes until new brood stocks were developed. Paired stockings were resumed in 1995 with releases of the Green Lake and Seneca strains, but those year-classes are not yet old enough to adequately evaluate relative survival. Thus, evaluation of stocking for the Midlake Refuge is limited to comparison of relative survival of the 1984–1985 year-classes of Marquette and Seneca strains stocked in 1985–1986.

Our objectives were to determine whether the relative abundance, survival, emigration, growth, and sea lamprey wounding rates differed between the 1984 and 1985 year-classes of Seneca and Marquette strains of lake trout stocked on the Sheboygan Reef in the southern refuge of Lake Michigan. Previously, evaluation of the relative performance of lake trout strains stocked in the southern refuge was not possible because insufficient time had elapsed since the fish were stocked. Herein, we describe relative abundance, survival, emigration, growth, and sea lamprey wounding rates of the 1984 and 1985 year-classes of Seneca and Marquette strain lake trout in fall gill-net assessments on the Sheboygan Reef and the Milwaukee near shore during 1987–2000.

## Methods

Each strain (Marquette and Seneca) and year-class (1984 and 1985) of lake trout stocked in each year (1985 and 1986) consisted of six different lots identified by removal of the adipose fin and insertion of coded wire tags (CWTs) into the cartilage of their snouts. All lake trout were transported via boat to the Sheboygan Reef for release from Lake Michigan ports (Table 1). In 1985, fish were transported from the Iron River National Fish Hatchery (IRNFH) in Iron River, Wisconsin, to Waukegan, Illinois, on May 30 and to Manitowoc,

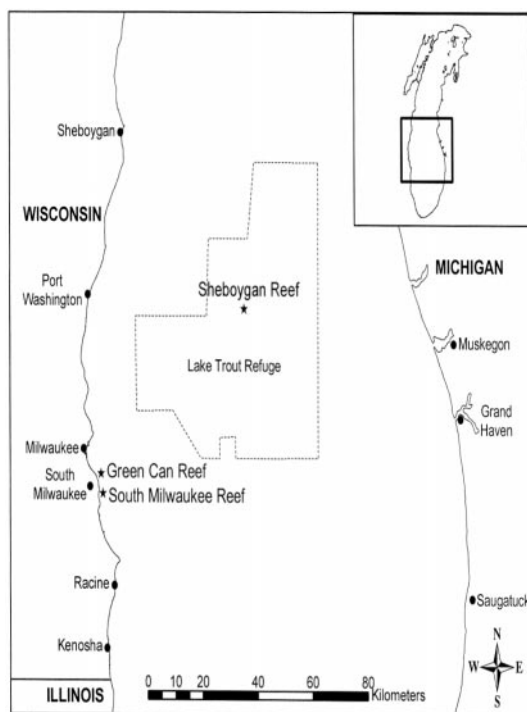


FIGURE 1.—Map of study area showing the extent and location in southern Lake Michigan of the Sheboygan Reef and nearshore Milwaukee reefs fished in fall gill-net assessments during 1987–2000.

Wisconsin, on 11–15 July, where trucks were loaded on the U.S. Coast Guard buoy tender *Mesquite* for transportation 125 km and 94 km, respectively, to the Sheboygan Reef. In 1986, fish were transported from IRNFH to Kewaunee, Wisconsin, where trucks were loaded on the car ferry *Badger* for transportation 125 km to the Sheboygan Reef on June 11 and 13.

The relative abundance of lake trout on the Sheboygan Reef was monitored with assessment gill nets fished during 1987–2000. The Sheboygan Reef, located in the northeast part of the Midlake Reef Plateau (Figure 1), rises upward and covers an area of about 65 km<sup>2</sup> at depths of 44–60 m (Miller and Holey 1992). Consequently, gill nets were fished on the top of the Sheboygan Reef at depths of 40–55 m. Commercial fishers were contracted to fish assessment nets during 1987–1997, and the state of Wisconsin RV *Barney Devine* fished in 1998–2000. Nets were constructed of multifilament nylon twine with 1.8-m-deep panels, ranging from 11.4- to 15.2-cm stretch mesh in 1.3-cm increments. Panel lengths of each mesh size were 30.5 m in 1987 and 1998–2000, and 76.0 m

TABLE 2.—Total number of lift-days and total effort (m) of multifilament nylon graded-mesh gill nets (11.4–15.2 cm in 1.3-cm increments) fished on the Sheboygan Reef and in the Milwaukee inshore in fall from 1987 to 2000. Each box of nets fished in 1987 and 1998–2000 was constructed of two 30.5-m panels of each mesh (244 m/box); each box fished from 1988 to 1997 had one 76.2-m panel of each mesh (305 m/box).

Year	Sheboygan Reef		Milwaukee inshore	
	Lift-days	Total effort (m)	Lift-days	Total effort (m)
1987	4	2,438	8	9,266
1988	2	1,829	5	5,486
1989	2	1,219	3	3,658
1990	4	4,267	4	4,877
1991	4	3,658	4	4,877
1992	4	4,267	4	4,877
1993	4	4,267	4	4,877
1994	3	2,438	4	4,877
1995	4	4,877	3	2,438
1996	5	6,096	2	2,438
1997	3	2,438	3	3,658
1998	2	975	2	1,951
1999	1	732	3	1,643
2000	1	488	3	1,951

during 1988–1997. In each year the total annual effort fished on 1–5 catch dates (24-h lifts) ranged from 488 to 6,096 m (Table 2).

To evaluate emigration inshore, the relative abundance of lake trout was monitored in the Milwaukee nearshore area with assessment gill nets comparable to those fished on the Sheboygan Reef over the same time period. The annual gill-net effort fished ranged from 1,643–9,266 m over 2–8 lift-days (Table 2). The Milwaukee nearshore area consists of a complex of nearshore reefs, 66 km from the Sheboygan Reef, adjacent to the south border of the City of Milwaukee (Figure 1). We fished two reefs within the nearshore area, known locally as the Green-Can Reef and the South Milwaukee Reef. These nearshore reefs are at shallow depth (6–10 m.) and consist of sand and limestone outcroppings of cobble and gravel (Marsden 1994). Fall fishing was conducted in this area to assess the spawning population of lake trout, sea lamprey wounding rates, and the movement or emigration of lake trout stocked on the Midlake Refuge, including fish stocked for strain evaluation, to the near shore.

Lake trout of the 1984 and 1985 year-classes of Seneca and Marquette strains were determined by the presence of a CWT. Lake trout captured by commercial contractors were iced in the nets and taken ashore, where they were examined 12–48 h later, whereas lake trout captured by the RV *Barney*

*Devine* were examined onboard. Total length (mm) and fin clip were recorded for all lake trout. Sea lamprey attachment marks were classified according to King (1980). Heads were removed from any lake trout with a missing adipose fin and frozen for later examination. Heads were later thawed and CWTs were extracted by dissection. Each CWT was examined under a dissecting microscope and the binary code was cross-referenced to its CWT lot code for determination of strain, age, and year-class.

Relative abundance was indexed as the numbers of the 1984 and 1985 year-classes of Marquette and Seneca strains captured at ages 3–16 per 305 m of gill net for each gang of nets lifted in each year during 1987–2000, corrected to a standard stocking of 200,000 yearlings. First, to account for variable tag retention among CWT lots, we multiplied the number stocked of each CWT lot by its tag retention rate, determined at the hatchery prior to stocking (effective number stocked). Second, to account for variable numbers stocked among CWT lots, we divided the effective number stocked per CWT lot into 200,000 (standardized number stocked). Third, to standardize numbers captured to numbers stocked, we multiplied the number captured of each CWT lot by the standardized number stocked (adjusted number captured). Fourth, we summed the adjusted number captured over all CWT lots for each strain and year-class. Last, to account for variable net lengths among lifts, we divided the adjusted number caught of each strain and year-class by the length of the net to determine relative abundance on each sampling date (catch per effort [CPE] = number per 305 m of gill net, corrected to a standard stocking of 200,000 yearlings).

We compared the relative abundance and mortality of age-3 and older lake trout between strains (Seneca and Marquette), year-classes (1984 and 1985), and recovery locations (Sheboygan Reef and nearshore Milwaukee area) using analysis of covariance (ANCOVA). For the analysis, we assumed that both strains and year-classes were equally vulnerable to capture in our sampling gear and used recovery locations to evaluate emigration from the Sheboygan Reef to the nearshore Milwaukee area. The ANCOVA was derived from the basic catch curve, with interactions for testing homogeneity of instantaneous total mortality rates ( $b_1$ ) among year-classes ( $b_2$ ), strains ( $b_3$ ), and recovery locations ( $b_4$ ) through the interactions between the covariate, age, and main effects, strains, year-classes, and recovery locations ( $b_5$ – $b_{15}$ ):

$$Y = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_1X_2 \\ + b_6X_1X_3 + b_7X_1X_4 + b_8X_2X_3 + b_9X_2X_4 \\ + b_{10}X_3X_4 + b_{11}X_1X_2X_3 + b_{12}X_1X_2X_4 \\ + b_{13}X_1X_3X_4 + b_{14}X_2X_3X_4 + b_{15}X_1X_2X_3X_4.$$

In the model,  $Y$  is the natural logarithm of the CPE at age  $t$  ( $\log_e[\text{CPE}_t + 1]$ ),  $b_0$  is the natural logarithm of the CPE at age 0 ( $\log_e[\text{CPE}_0 + 1]$ ),  $X_1$  is age  $t$  (ages 3–16 years),  $X_2$  is year-class (1984 or 1985),  $X_3$  is strain (Seneca or Marquette), and  $X_4$  is recovery location (Sheboygan Reef or nearshore Milwaukee area). Thus, the ANCOVA model is a catch curve with three additional factors and all possible interactions. We added one to each estimate of relative abundance because catches corresponded closely to relative abundance estimates (i.e., the addition of one to each estimate of CPE was equivalent to adding one to zero catches). Interactions were dropped from the model, if non-significant ( $P > 0.05$ ), before judging the significance ( $P \leq 0.05$ ) of main effects. Relative abundance was expressed as the geometric mean, with 95% confidence limits, back-transformed from natural logarithms into the original scale ( $\text{CPE} = \text{number per 305 m of gill net, corrected to a standard stocking of 200,000 yearlings}$ ).

To determine whether differences in growth between strains and year-classes affected vulnerability to capture, we compared von Bertalanffy growth parameters between the 1984 and 1985 year-classes of Marquette and Seneca strains of lake trout captured at ages 3–16 in fall assessment gill-net fishing during 1987–2000. First, we fitted growth curves to each strain and year-class, both strains combined, both year-classes combined, and all strains and year-classes combined. We estimated parameters ( $L_\infty$ ,  $K$ , and  $t_0$ ) and asymptotic standard errors (ASE) for the multiplicative error model because we used lengths of individual fish (Quinn and Deriso 1999). Next, we constructed likelihood ratio tests from the residual sums of squares and degrees of freedom of nested models to determine if growth differed between year-classes and strains. For example, to determine if growth differed between the 1984 and 1985 year-classes of Seneca strain lake trout, we constructed the likelihood ratio test from the residual sum of squares and degrees of freedom for the overall model for all Seneca strain lake trout (reduced model) and from the residual sums of squares and degrees of freedom for the two models for each year-class of Seneca strain lake trout (full model).

Last, we tested the significance of the reduction in the residual sums of squares between the full and reduced models using the  $F$ -ratio of the mean square errors for the full and reduced models (Bates and Watts 1988).

We compared the frequency of type A and B sea lamprey marks between Marquette and Seneca strains of lake trout captured on the Sheboygan Reef based on wounding data collected between 1994 and 2000. We considered sea lamprey wounding observations on lake trout made before 1995 to be unreliable because personnel making these observations were untrained in the mark classification system developed by King (1980). Few fish of the 1984 and 1985 year-classes were captured in the Milwaukee nearshore area during fall gill netting, so we compared wounding rates between Marquette and Seneca strains only for lake trout captured during fall gill netting on the Sheboygan Reef. To determine if wounding rates differed between Marquette and Seneca strains of lake trout on Sheboygan Reef, we used a  $2 \times 3$  chi-square contingency table to compare the frequency of occurrence of wounds (A1 through A3 wounds, summed) and marks (B1 through B4 marks, summed) between the two strains (Marquette and Seneca) among three size-classes (633–734, 735–836, and  $\geq 837$  mm) over all years sampled. We used the same size-classes and expressed wounding rates as the number of wounds per 100 fish, as standardized in the Great Lakes for reporting sea lamprey wounding rates (Eshenroder and Koonce 1984).

## Results

### Growth

On the Sheboygan Reef, differences between von Bertalanffy growth parameters for the Marquette and Seneca strains or the 1984 and 1985 year-classes of lake trout did not indicate that the two strains differed in their vulnerability to sampling in our gear. Within-strain growth did not differ significantly between the 1984 and 1985 year-classes of the Marquette strain ( $F_{3,1071}$ ,  $P = 0.194$ ), or of the Seneca strain ( $F_{3,475}$ ,  $P = 0.214$ ), or when both strains were combined ( $F_{3,1552}$ ,  $P = 0.145$ ). von Bertalanffy growth parameters were similar for  $K$  and  $t_0$  between Marquette strain lake trout ( $K = 0.135$ , ASE = 0.005;  $t_0 = 0.246$ , ASE = 0.068) and Seneca strain lake trout ( $K = 0.133$ , ASE = 0.007;  $t_0 = 0.267$ , ASE = 0.061). However, growth did differ significantly between the Seneca and Marquette strains of lake trout for the param-

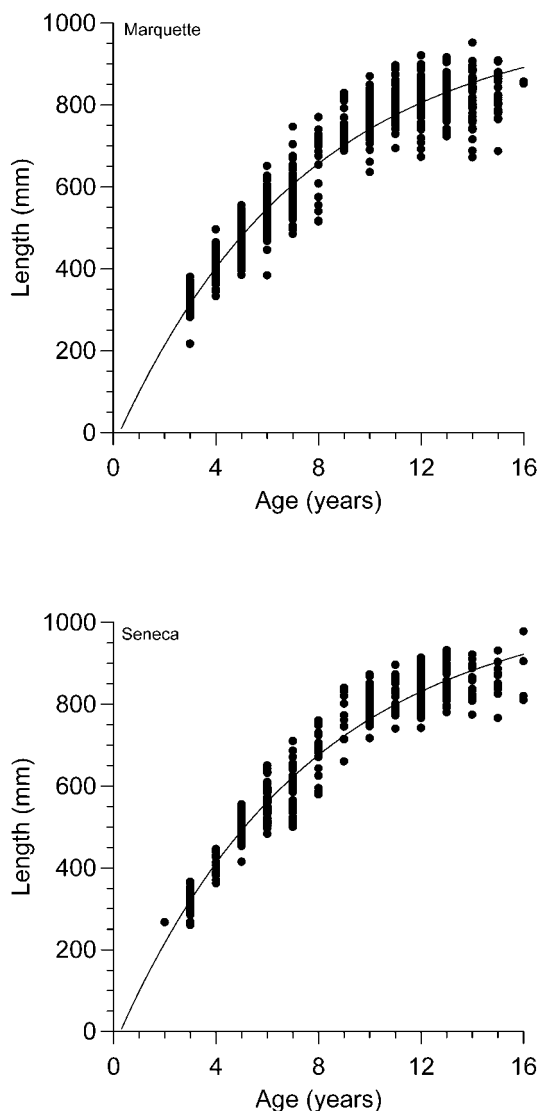


FIGURE 2.—Length at ages 3–16 of Marquette and Seneca strains of lake trout captured in fall gill-net assessments in Lake Michigan on the Sheboygan Reef during 1987–2000. The blackened dots show the lengths at capture for individual fish, and the curve depicts the von Bertalanffy growth curve.

eter  $L_{\infty}$  ( $F_{3,1552}$ ,  $P = 0.001$ ), which was slightly greater for Seneca strain lake trout ( $L_{\infty} = 1,052$  mm, ASE = 21.9 mm) than for Marquette strain lake trout ( $L_{\infty} = 1,012$ , ASE = 14.5 mm; Figure 2).

### Relative Abundance and Survival

Relative abundance was consistent between year-classes and strains on the Sheboygan Reef

TABLE 3.—Mean relative abundance (SDs in parentheses) of the 1984 and 1985 year-classes of Marquette and Seneca strain lake trout captured at ages 3–16 in fall gill-net assessments in Lake Michigan on the Sheboygan Reef (Sheb) and in the nearshore Milwaukee area (Milw) during 1987–2000. Relative abundance was indexed as the number captured per 305 m of gill net, corrected to a standard stocking of 200,000 yearlings.

Age	Marquette strain				Seneca strain			
	1984		1985		1984		1985	
	Milw	Sheb	Milw	Sheb	Milw	Sheb	Milw	Sheb
3	0.0 (0.0)	33.5 (2.8)	0.0 (0.0)	3.1 (0.4)	0.0 (0.0)	16.2 (2.2)	0.0 (0.0)	0.3 (0.5)
4	0.0 (0.0)	8.4 (5.0)	0.0 (0.0)	6.6 (1.3)	0.0 (0.0)	5.4 (0.8)	0.0 (0.0)	1.1 (1.8)
5	0.0 (0.0)	72.8 (1.2)	0.0 (0.0)	6.0 (2.9)	0.0 (0.0)	24.1 (2.4)	0.0 (0.0)	1.9 (1.5)
6	1.0 (0.2)	14.3 (5.4)	1.4 (1.1)	15.8 (2.1)	0.2 (0.3)	5.6 (3.8)	0.0 (0.0)	3.4 (1.8)
7	6.8 (0.2)	7.4 (1.2)	2.3 (0.8)	5.6 (1.5)	0.9 (0.8)	6.6 (1.0)	0.2 (0.3)	5.0 (0.6)
8	5.0 (0.5)	3.1 (0.8)	2.5 (0.9)	0.9 (0.6)	0.6 (0.3)	4.3 (0.3)	0.0 (0.0)	0.3 (0.8)
9	3.4 (2.0)	0.0 (0.0)	0.4 (0.5)	10.0 (1.4)	0.5 (0.6)	0.4 (0.8)	0.0 (0.0)	4.0 (0.6)
10	0.2 (0.3)	28.5 (1.1)	1.8 (0.1)	1.6 (1.0)	0.0 (0.0)	13.6 (0.6)	0.0 (0.0)	0.4 (0.5)
11	1.1 (1.0)	5.6 (1.1)	0.0 (0.0)	3.5 (0.5)	0.0 (0.0)	2.1 (1.3)	0.9 (1.6)	1.3 (1.2)
12	2.4 (0.5)	11.3 (1.0)	0.3 (0.5)	9.0 (0.2)	0.1 (0.1)	6.9 (1.0)	0.0 (0.0)	9.2 (0.2)
13	0.7 (0.6)	25.7 (0.3)	0.4 (0.6)	13.0 (1.0)	0.0 (0.0)	12.1 (0.4)	0.0 (0.0)	7.8 (0.2)
14	0.7 (1.1)	42.9 (0.2)	0.0 (0.0)	3.8	0.0 (0.0)	16.2 (0.2)	0.0 (0.0)	1.3
15	0.7 (1.2)	22.1	0.4 (1.1)	2.0	0.0 (0.0)	6.8	0.0 (0.0)	2.6
16	0.3 (0.8)	8.5			0.0 (0.0)	2.1		

and in the Milwaukee nearshore area because none of the three-way or four-way interactions were significant (age  $\times$  year-class  $\times$  strain  $\times$  location interaction:  $F_{1,353} = 0.779$ ,  $P = 0.378$ ; age  $\times$  year-class  $\times$  strain interaction:  $F_{1,354} = 0.910$ ,  $P = 0.341$ ; age  $\times$  year-class  $\times$  location interaction:  $F_{1,354} = 0.751$ ,  $P = 0.387$ ; age  $\times$  strain  $\times$  location

interaction:  $F_{1,354} = 0.253$ ,  $P = 0.264$ ; and year-class  $\times$  strain  $\times$  location interaction:  $F_{1,354} = 0.811$ ,  $P = 0.368$ ). Because all three-way and four-way interactions were not significant, we were able to interpret mean relative abundance through main effects and two-way interactions between strains, year-classes, and recovery locations.

The mean relative abundance of the 1984 and 1985 year-classes of Marquette and Seneca strains of lake trout varied erratically with age but did not decline with age on the Sheboygan Reef and Milwaukee nearshore area (age covariate effect:  $F_{1,363} = 0.259$ ,  $P = 0.611$ ; Table 3). Mean relative abundance over both strains, year-classes, and recovery locations declined from age 3 (1.2 fish) to age 4 (0.8 fish), increased to age 7 (3.4 fish), decreased to age 9 (1.1 fish), increased to age 12 (4.0 fish), and then declined through age 16 (0.6 fish; Figure 3). Consequently, we could not estimate total annual mortality for either year-class or strain in either capture area.

Marquette strain lake trout survived at a higher rate than Seneca strain lake trout prior to age 3 but at similar rates after age 3. Average survival of Marquette and Seneca strains of lake trout was similar after age 3 because the age  $\times$  strain interaction was not significant ( $F_{1,358} = 0.298$ ,  $P = 0.586$ ). Mean relative abundance of the Marquette strain (2.7 fish) was more than 2.1 times higher than that of the Seneca strain (1.3 fish) because the strain main effect was significant ( $F_{1,363} = 33.458$ ,  $P < 0.001$ ; Figure 4).

The 1984 year-class of lake trout survived at a

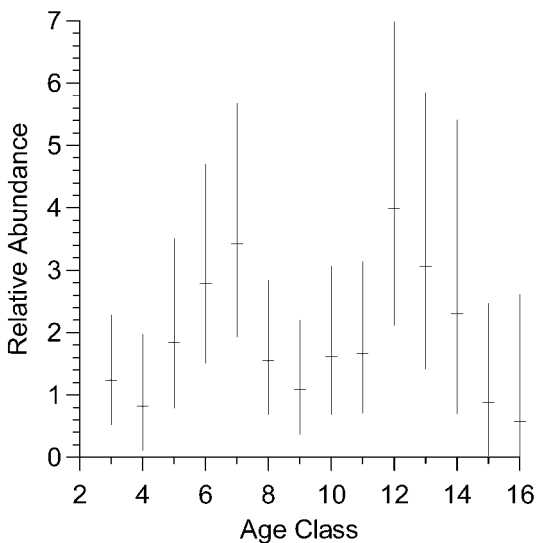


FIGURE 3.—Relative abundance (with 95% confidence intervals) of lake trout captured at ages 3–16 in fall gill-net assessments in Lake Michigan on the Sheboygan Reef and in the nearshore Milwaukee area during 1987–2000. Relative abundance was indexed as the number captured per 305 m of gill net, corrected to a standard stocking of 200,000 yearlings.

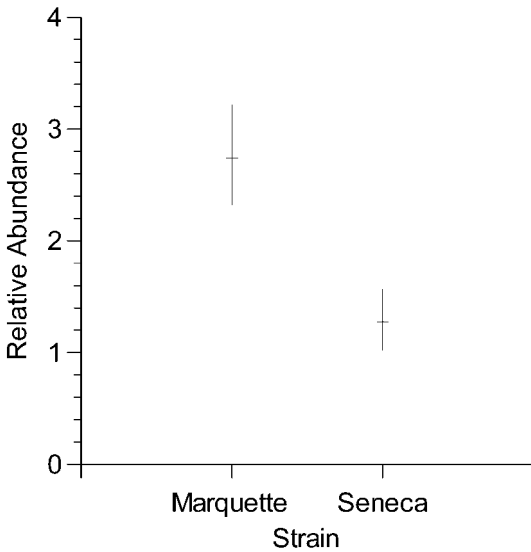


FIGURE 4.—Relative abundance (with 95% confidence intervals) of Marquette and Seneca strains of lake trout captured in fall gill-net assessments in Lake Michigan on the Sheboygan Reef and in the nearshore Milwaukee area during 1987–2000. Relative abundance was indexed as the numbers of the 1984 and 1985 year-classes captured per 305 m of gill net, corrected to a standard stocking of 200,000 yearlings.

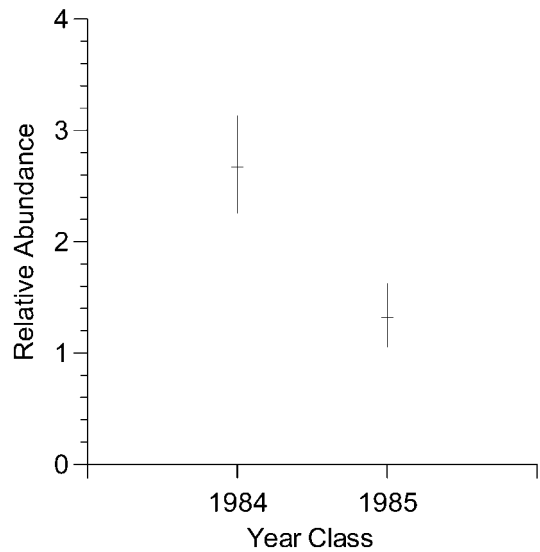


FIGURE 5.—Relative abundance (with 95% confidence intervals) of the 1984 and 1985 year-classes of lake trout captured in fall gill-net assessments in Lake Michigan on the Sheboygan Reef and in the nearshore Milwaukee area during 1987–2000. Relative abundance was indexed as the numbers of Marquette and Seneca strains captured per 305 m of gill net, corrected to a standard stocking of 200,000 yearlings.

higher rate than the 1985 year-class of lake trout prior to age 3 but at similar rates after age 3. Average survival of the 1984 and 1985 year-classes of lake trout was similar after age 3 because the age  $\times$  year-class interaction was not significant ( $F_{1,358} = 0.540$ ,  $P = 0.463$ ). In contrast, mean relative abundance of the 1984 year-class (2.7 fish) was nearly 2.0 times higher than that of the 1985 year-class (1.3 fish) because the year-class main effect was significant ( $F_{1,363} = 27.844$ ,  $P < 0.001$ ; Figure 5). Differences in mean relative abundance between Marquette and Seneca strains of lake trout were similar between the 1984 and 1985 year-classes (strain  $\times$  year-class interaction:  $F_{1,358} = 0.002$ ,  $P = 0.966$ ).

#### Emigration

Emigration of lake trout from the Sheboygan Reef to the nearshore Milwaukee area was similar for the Marquette and Seneca strains but higher for the 1984 year-class than the 1985 year-class. Average survival of stocked lake trout was similar on the Sheboygan Reef and the nearshore Milwaukee area (age  $\times$  location interaction:  $F_{1,358} = 0.918$ ,  $P = 0.339$ ), but mean relative abundance of lake trout was more than 14.4 times higher on

the Sheboygan Reef (5.2 fish) than in the nearshore Milwaukee area (0.4 fish; location main effect:  $F_{1,363} = 11.867$ ,  $P < 0.001$ ; Figure 6). Emigration from the Sheboygan Reef to the nearshore Milwaukee area was similar between strains because differences in mean relative abundance between Marquette and Seneca strains of lake trout were similar in the two areas (strain  $\times$  location interaction:  $F_{1,358} = 0.354$ ,  $P = 0.552$ ). In contrast, mean relative abundance of the 1984 year-class (8.1 fish) was more than 2.4 times greater than the 1985 year-class (3.3 fish) on the Sheboygan Reef, whereas mean relative abundance of the 1984 year-class (0.5 fish) was only 1.9 times greater than the 1985 year-class (0.3 fish) in the nearshore Milwaukee area because the year-class  $\times$  location interaction was significant ( $F_{1,358} = 11.888$ ,  $P \leq 0.001$ ; Figure 7).

#### Sea Lamprey Wounding

On the Sheboygan Reef, sea lamprey wounding rates did not differ significantly between the Marquette and Seneca strains of lake trout among size-classes (633–734, 735–836, and  $\geq 837$  mm) during 1994–2000 (Table 4). Wounding rates did not differ significantly between strains among size-classes

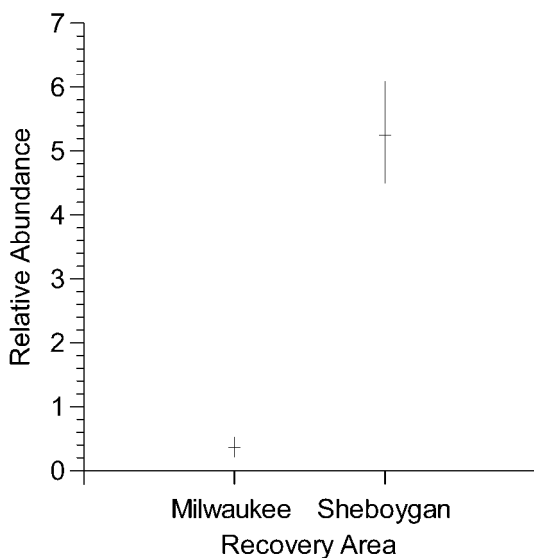


FIGURE 6.—Relative abundance (with 95% confidence intervals) of lake trout captured in fall gill-net assessments in Lake Michigan on the Sheboygan Reef and in the nearshore Milwaukee area during 1987–2000. Relative abundance was indexed as the numbers of Marquette and Seneca strains captured per 305 m of gill net, corrected to a standard stocking of 200,000 yearlings.

ses for type A1–A3 wounds ( $\chi^2 = 1.536$ ,  $df = 2$ ,  $P = 0.464$ ) or type B1–B4 marks ( $\chi^2 = 3.563$ ,  $df = 2$ ,  $P = 0.168$ ).

### Discussion

#### Strain Differences

The greater abundance and survival of the Marquette strain that we observed was not caused by differences in size at stocking, differential growth between the two strains after stocking that led to different catchability, or a higher emigration rate away from the Sheboygan Reef by the Seneca strain. Size at stocking of the two strains was similar, so neither strain would have experienced a survival advantage based on size at release. Growth of the two strains differed significantly after stocking, but the difference was only biologically slight. Returns of the Marquette strain of lake trout were greater than the Seneca strain lake trout in angling fisheries in both Wisconsin and Michigan waters (Wisconsin Department of Natural Resources, unpublished data; J. Clevenger, Michigan Department of Natural Resources, unpublished data). The abundance of both strains in the Milwaukee nearshore area was low, which suggests that emigration from the Sheboygan reef to nearshore waters was low.

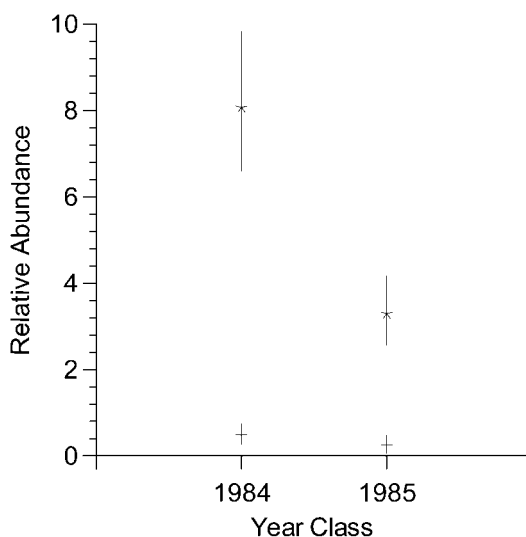


FIGURE 7.—Relative abundance (with 95% confidence intervals) of the 1984 and 1985 year-classes of lake trout captured in fall gill-net assessments in Lake Michigan on the Sheboygan Reef (“picnic table” symbols) and in the nearshore Milwaukee area (simple horizontal bars) during 1987–2000. Relative abundance was indexed as the numbers of Marquette and Seneca strains captured per 305 m of gill net, corrected to a standard stocking of 200,000 yearlings.

We could not evaluate why or when the Marquette strain survived better than the Seneca strain prior to age 3 because our assessment gear did not capture lake trout younger than age 3. In Lake Ontario, year-class strength was established within the first year after stocking (Elrod et al. 1989, 1995). Following the survival of six paired lots of lake trout reared at two densities, mortality between the two groups stopped changing 2 months after stocking (Elrod et al. 1989). Differences in mortality between groups stocked in different seasons by different techniques for paired stocking at

TABLE 4.—Sea lamprey wounding rates (expressed as the total number of A1–A3 wounds and B1–B4 marks per 100 fish) for the 1984 and 1985 year-classes of Seneca and Marquette strains of lake trout captured during 1994–2000 in fall gill-net assessments on the Sheboygan Reef in the southern refuge of Lake Michigan. See text for an explanation of wound and mark types.

Length (mm)	A1–A3 wounds		B1–B4 marks	
	Marquette	Seneca	Marquette	Seneca
633–734	2.4	0.0	21.4	0.0
735–836	12.9	14.0	18.8	17.0
≥837	14.8	3.9	84.3	46.8
Total	12.4	9.4	35.9	29.4

20 sites over 4 years occurred in the first year following stocking (Elrod et al. 1995).

Our results are in contrast with those of other studies in the Great Lakes, in which the Seneca strain experienced higher survival after age 3 than the Marquette strain (Elrod et al. 1995; McClain et al. 1996). In both Lake Huron and Lake Ontario, Seneca strain lake trout are significantly better at avoiding sea lamprey attack than Marquette strain lake trout (Schneider et al. 1996; Madenjian et al. 2004). Sea lamprey wounding rates on lake trout are much lower in southern Lake Michigan than in either Lake Huron or Lake Ontario, presumably due to a lower abundance of parasitic sea lampreys in southern Lake Michigan (Hansen 1999). Our results indicate that both sea lamprey wounding rates and the survival rates of age-3 and older lake trout did not differ significantly between Seneca strain and Marquette strain lake trout in the mid-lake refuge of Lake Michigan. Thus, our findings corroborated the contention that the higher survival of Seneca strain lake trout, compared with that of Marquette strain lake trout, was attributable to the ability of Seneca strain lake trout to better avoid sea lamprey attack.

#### *Year-Class Differences*

The reason for the difference in survival between the 1984 and 1985 year-classes is not obvious. Based on hatchery records, stress during transportation to the stocking site may have caused poorer survival of the 1985 year-class because a portion of the 1985 year-class were observed sick or dying and were released (at the dock or in the lake) prior to reaching the Sheboygan Reef stocking site in an effort to ensure the remaining fish would survive to the stocking site (National Fish Hatchery, unpublished data). No such observations of stress were recorded for the 1984 year-class.

Even in the absence of differences in handling stress, early year-classes often survive at higher rates than later year-classes of lake trout stocked in the Great Lakes. For example, relative abundance of stocked lake trout declined, despite relatively consistent stocking rates, because survival in the first 1–2 years after stocking declined in Lake Superior (Hansen et al. 1994), Lake Ontario (Elrod et al. 1993), and Lake Huron (Wilberg et al. 2002). Studies in other Great Lakes suggest that the survival of later year-classes of stocked lake trout declined because of competition with or predation by earlier year-classes (Elrod et al. 1993; Hansen et al. 1994), though fishing mortality con-

tributed to declining survival in some areas of Lake Superior (Hansen et al. 1996) and sea lamprey mortality contributed to declining survival in some areas of Lake Huron (Wilberg et al. 2002). In the southern refuge of Lake Michigan, neither commercial nor recreational fishing is permitted, so fishing mortality did not likely cause survival of the 1985 year-class to be lower than that of the 1984 year-class. Rather, competition with or predation by earlier year-classes may have limited the survival of the 1985 year-class (compared with the 1984 year-class) because total densities of lake trout on the Sheboygan Reef were among the highest in the Great Lakes (Hansen 1999).

#### *Age Differences*

Our results suggest that the relative abundance of lake trout in the southern refuge of Lake Michigan did not decline with age, which is inconsistent with the pattern of decreasing abundance with increasing age that we expected (Ricker 1975; Quinn and Deriso 1999). For catch curves based on cohorts or year-classes, variation in catchability through time could cause catches of year-classes to increase, rather than decrease, with age (Quinn and Deriso 1999). An increase in catchability through time could be the result of a change in behavior of the organism (e.g., shift in the spawning period) that increased the vulnerability of the species to capture in the gear through time (Ricker 1975; Quinn and Deriso 1999).

We have no evidence that suggests lake trout behavior changed systematically on the Sheboygan Reef during 1987–2000. Gill nets used to index the abundance of spawning lake trout were set in the same locations at the same time of year, each year during the study period. In addition, the number of days fished in any given year ranged from only 1–5 d during the 14-year period, whereas the spawning season for lake trout can extend longer than 1 month in the Great Lakes (Eschmeyer 1957). We caught lake trout in spawning condition throughout the sampling period from mid-October to mid-November, with the largest numbers of all age groups caught in the middle of the sampling period (Wisconsin Department of Natural Resources, unpublished data). Of 43 total lift-days fished during the 14-year period, 34 (79%) occurred between October 24 and November 7, so we do not believe that the trend in CPE we observed was an artifact of the low frequency of our sampling in relation to a long-term trend in the spawning period. More likely, the apparent lack of a decline in estimated relative abundance with age

was an artifact of measurement error (e.g., small numbers of samples).

### Management Implications

Our findings suggest that the year-class strength of Marquette and Seneca strain lake trout was established prior to age 3 and that under conditions of low sea lamprey abundance and mortality, age-3 and older Marquette strain lake trout survived to the same degree as Seneca strain lake trout, even in a deepwater environment such as the Midlake Reef Plateau. Under conditions of relatively low sea lamprey abundance and low fishing mortality, managers can expect that stocking both strains will result in the development of old, mature fish at spawning time. Managers should not expect a difference in growth or movement between these two strains when stocked in the same location. Stress during transportation to the stocking site can have a significant effect on survival of stocked lake trout regardless of strain, so future evaluations of rehabilitation strategies in Lake Michigan should explicitly account for stress during transportation.

We were unable to compare the reproductive contributions by these two strains because we have not yet detected progeny from mating of stocked lake trout on the Sheboygan Reef. Consequently, we do not know if one strain contributes more to reproduction than the other strain. Seneca strain lake trout produced a disproportionately greater percentage of fry than other strains on Stony Island Reef in Lake Ontario (Perkins et al. 1995) and on Six Fathom Bank in Lake Huron (Page et al. 2003). Greater contribution to reproduction by Seneca strain lake trout in Lake Ontario and Lake Huron is largely due to higher adult survival, which leads to greater numbers of large, old adults that contribute substantially more eggs toward the recruitment of fry (Madenjian et al. 2004). If a similar pattern holds true on the Sheboygan Reef in the future, then we expect the Marquette strain of lake trout to produce more fry than the Seneca strain of lake trout because the Marquette strain of lake trout is present in greater numbers at older ages than the Seneca strain of lake trout.

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